

Litho-refugia: the importance of rock landscapes for the long-term persistence of Australian rainforest fauna

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ABSTRACT

Rainforest was formerly widespread on the Australian continent but underwent large-scale contraction to pockets on the east coast through the Miocene and Quaternary. This contraction was due to increasingly dry and seasonal climatic conditions across the continent, which reached greatest severity during the glacial cycles of the Pleistocene. Extensive areas of exposed, layered rock in the mesic areas of Australia provide similar microclimatic conditions to rainforest, in being cool, moist and largely sheltered from fire. These rock habitats are stable and relatively buffered from short- and long-term climatic changes. Therefore, rock habitats can act as refugia (litho-refugia) for the persistence of rainforest lineages in areas where rainforest is currently, or was historically, marginal or absent. Here we outline a number of examples of rainforest faunal groups, primarily from mid-eastern and northeastern Queensland, that exemplify the importance of rock landscapes in the persistence of rainforest lineages.

Key words: climate change, microclimate, vertebrates, invertebrates

Introduction

Phylogeographic studies on rainforest vertebrates in eastern Australia repeatedly identify a pattern of historic reduction and sub-division of rainforest habitat (Schneider *et al.* 1998; Stuart-Fox *et al.* 2001; Hoskin *et al.* 2003; Moritz *et al.* 2005). Rainforest was widespread across the Australian continent until the early Miocene but then contracted through the Miocene and Quaternary due to a climatic shift to increasingly arid and seasonal conditions (Adam, 1992; Truswell 1993; Greenwood and Christophel 2005). In particular, rainforest was reduced to relatively small, isolated refugia along the east coast during the glacial periods of the Pleistocene (Webb and Tracey 1981; Kershaw 1994; Kershaw *et al.* 2005; Moritz *et al.* 2005). Dry glacial periods caused rainforest to contract to “edaphically or topographically wetter pockets in the regional vegetation mosaic” (Greenwood and Christophel 2005). This large-scale reduction in rainforest distribution had profound impacts on the rainforest-associated flora and fauna, with local extinctions, changes in species distributions and genetic diversity, and greatly altered regional patterns of community composition and species diversity (Adam 1992; Moritz *et al.* 2005; Schneider and Williams 2005; Hocknull *et al.* 2007).

Given the scale of historic reduction in rainforest area, the persistence of rainforest lineages is of particular interest. Current primary ‘refugia’ are the large blocks of rainforest along the east coast, particularly those with extensive upland areas (Webb and Tracey 1981; Adam 1992; Moritz *et al.* 2005). These areas currently display high species diversity and phylogenetic diversity (Moritz *et al.* 2005). However, rainforest lineages have also persisted in other areas, including small and isolated pockets of wet and ‘dry’ rainforest and boulder fields. An array of factors allowed

particular rainforest lineages to persist in particular locations, but here we highlight rock as an important factor. By ‘rock’ we refer to extensive, exposed areas of layered rock, such as boulder fields, boulder-strewn slopes and creek-lines, and heavily eroded escarpments. These rock areas may be within, or outside of, rainforest. The rainforest/rock floral associations are well recognised (Webb and Tracey 1981), but, to date, the faunal associations (with the exception of cave-dwelling invertebrates; Eberhard and Humphreys 2003; Richards 1987) have received less attention (Schuster 1981; Stanisic 2006). Here we focus on rock in the broader landscape and outline examples of both vertebrate and invertebrate groups that demonstrate the importance of rock for the persistence of rainforest lineages.

Extensive areas of exposed, layered rock in mesic regions of Australia offer cool, moist microhabitat similar to that found in rainforest. This rock habitat is a stable, long-term habitat that is relatively buffered from short and long-term variation in temperature and moisture. It is also largely immune to burning, a factor that greatly influences the distribution of rainforest in Australia (Adam 1992). Therefore, areas of extensive layered rock (‘litho-refugia’) have the potential to enhance the chances of persistence of rainforest lineages within a region. Persistence is a result of both favourable microclimatic conditions in the rock and the ability to exploit new niches. Here we concentrate on the favourable climatic conditions and only touch on the obviously intertwined topic of adaptation to rock habitat. We are particularly interested in considering situations in which rainforest lineages have persisted in rock despite the fact that rainforest vegetation is currently absent or marginal in the area, or was likely marginal or absent for periods in the past.

Examples

The examples provided herein are primarily from eastern Queensland (Fig. 1), a region in which rainforest is currently restricted to isolated blocks (Adam 1992). We selected taxa that satisfy one or more of the following criteria: (a) taxa that occur in rock but also show strong rainforest associations, (b) species for which relationships can be inferred from existing phylogenies and the rock dwellers have close affinities to taxa that are rainforest obligates, and (c) species that exist in isolated rock habitats that also support other groups with rainforest associations. Additionally, we have focussed on species with low dispersal capabilities to emphasise *persistence* versus potential recolonisation. This is not an exhaustive list and the same principles apply to many other elements of the Australian fauna and flora. An outstanding example is the Wollemi Pine (*Wollemia nobilis* Jones, Hill and Allen 1995), a gymnosperm that was widespread in Cretaceous rainforests but only persists as three tiny populations sheltered in deep, narrow sandstone gorges west of Sydney (Jones, Hill and Allen 1995; Hill 2003).

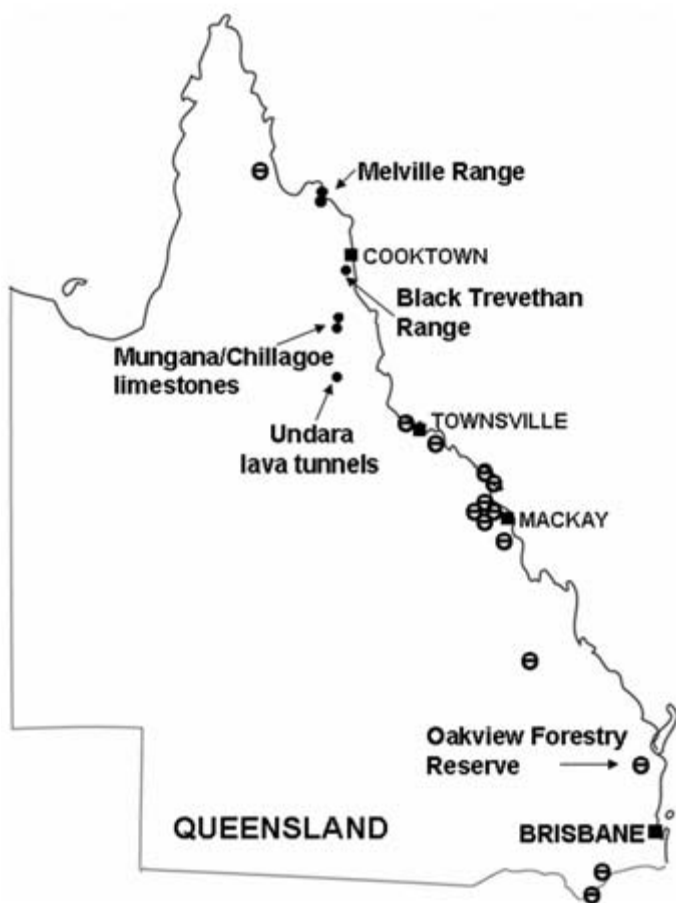


Figure 1. Map of Queensland showing the distribution of localities discussed in this paper. ■ = Towns, • = specific locality, ⊕ = significant rock habitat supporting leaf-tailed geckos.

Vertebrates:

The boulder mountain frogs of north Queensland

The microhylid frog genus *Cophixalus* Boettger 1892 is represented by 14 species in Australia, the majority of which inhabit high-altitude (approximately > 800 m) rainforests in northeastern Queensland. However, two species, *C. saxatilis* Zweifel and Parker 1977 and *C. zweifeli* Davies and McDonald 1998 stand alone in inhabiting sparsely vegetated boulder mountains surrounded by open forest communities. The former is narrowly endemic to the Black Trevethan Range (also known as Black Mountain), near Cooktown (Fig. 2A, 15° 40'S, 145° 16'E), the latter to the Melville Range (14°15'S, 144°28'E). Both are unusually large and show a high degree of similarity in morphology (Davies and McDonald 1998), despite the fact that genetic data show them not to be sister species (Hoskin 2004). The two species are only distantly related; with both being more closely related to rainforest species than to each other (Hoskin 2004). *Cophixalus zweifeli* is a sister species to *C. infacetus* Zweifel 1985 (from rainforests between Cairns and Cardwell (16°55'S – 18°16'S), and the affinities of *C. saxatilis* (Fig. 2B) lie with the clade comprising *C. bombiens* Zweifel 1985, *C. exiguus* Zweifel and Parker 1969 and *C. aenigma* Hoskin 2004 (from rainforests between Cooktown and Cairns; 15°28'S - 16°55'S). The large size and other novel characteristics of *C. saxatilis* and *C. zweifeli* have been attributed to convergent adaptation to isolated boulder piles (Hoskin 2004; Hoskin *et al.* in preparation).

In addition to *C. zweifeli*, the Melville Range is also home to another highly distinctive frog species with clear ties to past rainforests associations. Preliminary genetic studies on *Litoria andirrmalin* McDonald 1997 show the affinities of this species to lie with the *L. lesueuri* group (S. Donnellan pers. comm.), of which the most geographically proximate member, *L. jungguy* Donnellan and Mahony 2004 of north Queensland, inhabits rainforest (Donnellan and Mahony 2004). Interestingly, as with the rock-dwelling *Cophixalus* spp, this species is considerably larger than its closest relatives: *L. andirrmalin* max SVL 102 mm (McDonald 1997) vs 52.5 mm *L. lesueuri* Duméril and Bibron 1841, 69 mm *L. wilcoxii* Günther 1864, 71 mm *L. jungguy* (Donnellan and Mahony 2004).

The leaf-tailed geckos

The leaf-tailed geckos (*Orraya*, *Phyllurus* and *Saltuarius*) of eastern Australia provide an excellent example of a rainforest group that has largely shifted to rock. Of sixteen described species, ten, including the basal lineage *Orraya occultus* (Couper, Covacevich and Moritz 1993) (Fig. 3A), are tied exclusively to rock; seven to narrow outcrops with rainforest settings; and three to extensive rock in open forests (Couper *et al.* 1993, 1997, 2000, 2008a and b; Hoskin *et al.* 2003). A further two species have both rock- and tree-dwelling populations. The rock/rainforest connection is best seen in Queensland *Phyllurus* spp (southern Paluma Range – Kilkivan; 19°17'S – 26°08'S). Of eight species, six are tied exclusively to rock and these are all narrowly restricted within rainforest settings. The

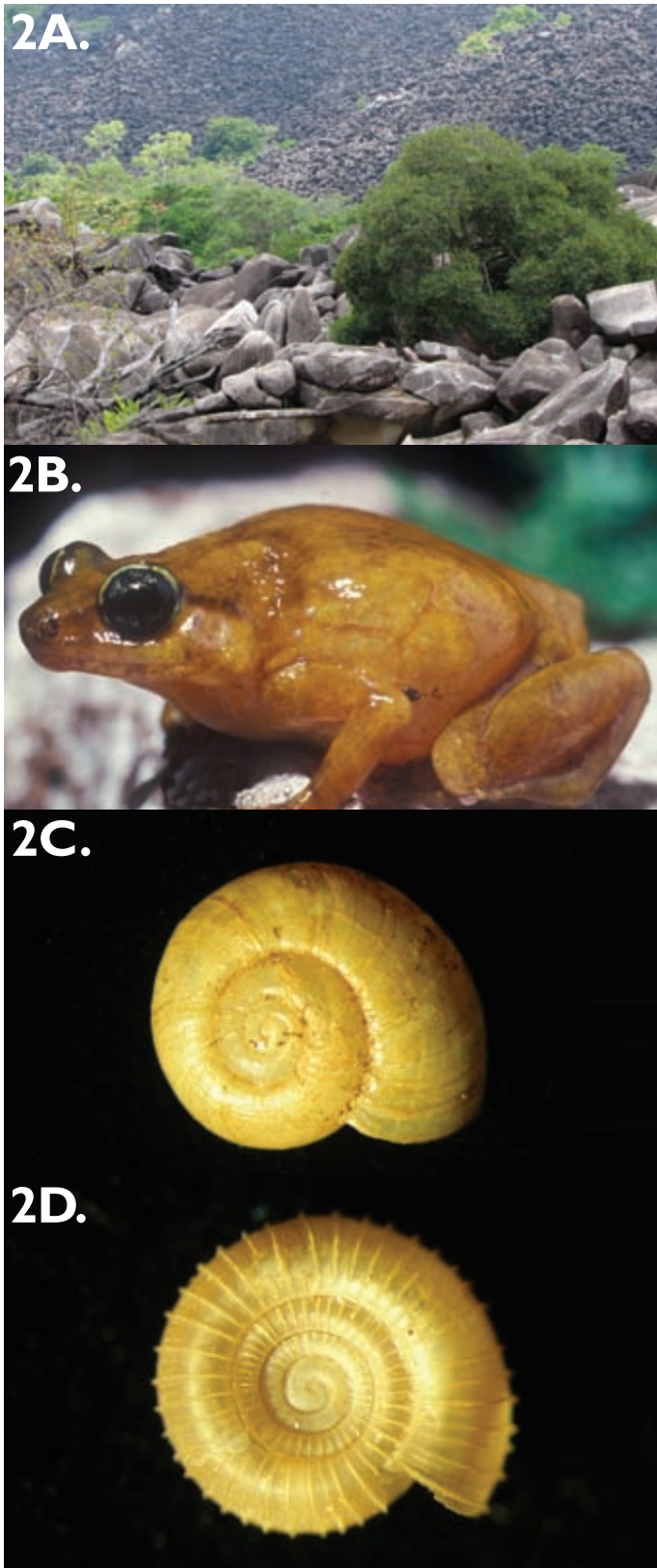


Figure 2. The Black Trevethan Range (also known as Black Mountain), a boulder mountain in northeastern Queensland supporting mesic-adapted fauna. Typical boulder habitat (A); the microhylid frog, *Cophixalus saxatilis* (B); *Saladelos commixta* (C); an undescribed charopid with affinities to high-altitude charopids in the rainforests of the northern Wet Tropics (D). Images; C. Hoskin (A); G. Cranitch (B), P. Couper (C) and (D).



Figure 3. Narrowly endemic leaf-tailed geckos tied to rock habitats. *Orraya occultus* from boulder-strewn creek-lines in the McIlwraith Range, northeastern Queensland (A) and *Phyllurus kabikabi* from a deep layer of broken volcanic rock capping a ridge summit in Oakview Forest Reserve, southeastern Queensland (B). Images; J. Wright (A), G. Cranitch (B).

most recently described *Phyllurus*, *P. kabikabi* Couper, Hamley and Hoskin 2008 (Fig. 3B, from Oakview State Forest/Forest Reserve; 26° 07' 23"S, 152° 19' 01"E) may have a total distribution not exceeding 6 hectares (Couper *et al.* 2008a). Couper *et al.* (2008b) argue that past climate change initiated the shift from trees to rock in ancestral leaf-tails. Populations of leaf-tailed geckos were 'squeezed' to fragmented forest remnants, 'The small size of these habitats, coupled with the drier conditions during changed climatic regimes, created selection pressures that favoured occupation of rocky habitats...' (Couper *et al.* 2008b). In these situations, layered, or deeply fissured rock, is likely to provide a more stable micro-habitat than the overlying forest.

The ring-tailed geckos

Cyrtodactylus Gray 1827 is a large genus comprising more than 80 species ranging across Southeast Asia, New Guinea, western Melanesia and northern Australia (Aaron Bauer 2003; Kraus and Allison 2006). Most species are found in humid forest, often in or around karst outcrops (Bauer pers. comm. 2007) when those are available. Within Australia, there is only one recognised species, *C. tuberculatus* (Lucas and Frost 1900), removed

by Wells and Wellington (1984; also see Rösler et al., 2007) from the synonymy of *C. lousiadensis* (De Vis 1892). These two species are morphologically similar, with the latter occurring in New Guinea and likely to consist of a complex of geographically separate species (Kraus and Allison 2006). *Cyrtodactylus tuberculatus* (confined to Australia) is known from dry tropical woodlands, vine thickets and rainforests (Wilson 2005). Yet, its distribution is highly fragmented and there is a strong association with rock at most collection sites. New Guinean members of the '*C. lousiadensis*' group appear to be obligatory rainforest taxa. Fred Kraus (pers. comm. 2007) reports collecting five species within this complex from primary or advanced secondary rainforest.

The current fragmented distribution of *C. tuberculatus* populations and their strong association with rock points to a distribution shaped by past climate change. In view of the habitat preferences of New Guinean '*C. lousiadensis*', it seems reasonable to surmise that *C. tuberculatus* was once more widespread and retreated to rock in response to past climate change. That this species co-occurs with other rainforest taxa that have shifted to rock (*Orraya occultus*, McIlwraith Range; *Cophixalus saxatilis*, land snails and arachnids in the Black Trevethan Range; *Cophixalus zweifeli*, Melville Range; land snails and a spider in the Chillagoe limestones) further supports this view.

The Rock Ringtail Possum

In discussing the relationships of Australian ringtail possums, Archer and Hand (2006) highlight the close relationship of *Petropseudes dahli* (Collett 1895) to *Pseudochirops archeri* (Collett 1884). *Petropseudes dahli* (Fig. 4B) is a rock obligate associated with deeply fissured rock and large boulders (Kerle and Winter 1995) in the Kimberley (WA) and from Arnhem Land (NT) through to northwestern Queensland. *Pseudochirops archeri* inhabits high-altitude rainforests of the Wet Tropics region of northeastern Queensland (Winter and Goudberg 1995). The inferred relationship between *P. dahli* and *P. archeri* is based on similarities in their dental morphology (Roberts et al. 2007; Scott Hocknull pers. comm.) Interestingly, neither species constructs a nest but instead roosts during the day on a rock ledge (*P. dahli*; Kerle and Winter 1995) or branch (*P. archeri*; Winter and Goudberg 1995), behaviour unique amongst modern Australian pseudocheirids.

Pseudochirops-type ringtails are represented in the Riversleigh rainforest faunas of north-western Queensland from the Late Oligocene to the Mid Miocene (Archer and Hand 2006). They disappeared abruptly at a time when climate change caused rainforest communities to decline widely (Merrick et al. 2006). Shortly thereafter, *Petropseudes* appeared in the fossil record (Pliocene) as the first arid habitats develop (Merrick et al. 2006). The timing of these events would suggest that *Petropseudes* evolved from a widespread *Pseudochirops* – like ancestor and that *P. dahli* can be traced to ancestral *Pseudochirops* populations that made an adaptive shift from rainforest trees to rock. This transition occurred in the rock-rich landscapes of northern Australia, which have massive sandstone escarpments (Fig. 4A) and extensive gorge systems.



Figure 4. Weathered sandstone of the Arnhem Escarpment (A), home of the Rock Ringtail Possum, *Petropseudes dahli* (B), a species with clear affinities to the Green Ringtail, *Pseudochirops archeri*, of the Wet Tropics rainforests.

Photos; A. Amey (A), Belinda Wright (B).

Invertebrates:

Queensland land snails

The Mungana - Chillagoe area (17°06'S - 17°09'S) of far northern Queensland features numerous limestone towers associated with dense vine thickets. These are part of the larger Chillagoe Formation, which extends beyond the Walsh River and becomes particularly prominent between the Mitchell and Palmer Rivers to the north-west (Stanisic 2005). This area boasts a rich land snail fauna (31 species in or around the rock formations) and features a number of narrow endemics (e.g. *Georissa minuta* (Odhner 1917) and *Pleuropoma extincta* (Odhner 1917)). The distribution of limestone outcrops and their associated snail faunas is patchy, with intervening expanses of inhospitable countryside (Stanisic 2006). The snails favour moist retreats within these rock formations, with the majority of species living under limestone talus, between fallen leaves and under rotten logs. There are also species that live on the limestone rocks - keeping to drip-lines and shaded situations (Stanisic 2006). Some of the taxa (*Saladelos* spp., *Pleuropoma* spp. and members of the family Charopidae) in this suite of 'rock snails' have close affinities with groups currently found in moist rainforests of eastern Australia (J. Stanisic pers. comm.) They are essentially a mesic fauna that became restricted to rock by climatic attrition (Stanisic 2006) and the associated decline of formerly widespread rainforest communities.

Some of the land snails inhabiting the boulder cavities within the Black Trevethan Range also have affinities with mesic rainforest faunas (e.g. *Saladelos commixta* Iredale 1933, QM MO 78702, Fig. 2C) and a large, undescribed species of charopid (QM MO 78703, Fig. 2D). The former is most closely related to species that inhabit rainforests and vine thickets in tropical and subtropical eastern Australia (John Stanisic pers. comm.), and the latter has a biconcave shell whose sculptural features are clearly related to species found in high-altitude rainforests of the northern Wet Tropics (e.g. Thornton Peak - 16°10'S, 145°23'E; Mount Hemmant - 16°07'S, 145°25'E and Mt Lewis - 16°35'S, 145°17'E; John Stanisic pers. comm.).

Arthropods

A number of arthropod genera have classic rock/rainforest distributions. For example, 14 of the 16 species of spiders belonging to the genus *Amauropelma* Raven and Stumkat 2001 (Ctenidae) inhabit mesic rainforest communities in northeastern Queensland. The remaining two species occur in mesic niches within different habitat types. One, *A. rifleck* Raven, Stumkat and Gray, 2001, is found in dense grassy cover in open forest communities in northeastern Queensland. The other, *A. undara* Raven, Stumkat and Gray 2001, is narrowly restricted to caves associated with the Undara lava tunnels (north-west of Townsville, NEQ). The complete absence of eyes in this species points to its adaptation to deep caves. All *Amauropelma*, except *A. undara*, are found in, or in close proximity to, the rainforests of northeastern Queensland. The distribution of *A. undara* is subcoastal and widely

disjunct (approximately 180 km inland, Raven *et al.* 2001). The Dry vine thickets associated with the rock formations at Undara point to past connections with more widespread mesic rainforest communities.

The boulder cavities within the Black Trevethan Range contain an assemblage of arthropods with strong ties to mesic rainforest communities. The following are some examples. A population of a gradungulid spider (Araneae: Austrochiloidea) currently referable to *Macrogradungula moonya* Forster, Platnick and Gray 1987 (QM S 78523) occurs in the Black Mountain boulder-fields. This species occurs in three disjunct populations (which may not be conspecific but further taxonomic assessment is hampered by the absence of males in collections), all associated with rock. The other populations are within rainforest communities in the Wet Tropics - sink holes in the Walter Hill Range - 17°47'S, 145°49'E, (Geoff Monteith pers. comm.) and caves and cavities in the boulder fields at the summit of Mount Bartle Frere - 17°24'S, 145°49'E (Geoff Monteith pers. comm.). This genus belongs to a primitive group of araneomorph spiders (Forster *et al.* 1987) found in Australia and New Zealand that are mostly associated with mesic forests (Robert Raven pers. comm.).

The second example is a large, undescribed tail-less whip scorpion (Order Amblypygi) (QM S 78516) that is restricted to the Black Mountain boulder-fields. This species' congeners are all associated with rainforests of Iron Range (12°44'S, 143°17'E) and McIlwraith Range (13°50'S, 143°17'E) on Cape York Peninsula and lowland rainforests of the Wet Tropics region (15°28' - 19°16'S). The rainforest species are generally found beneath bark or under litter and rocks with close ground contact (Geoff Monteith pers. comm.).

The final example is an undescribed idiopid spider belonging to the genus *Homogona* Rainbow 1914 (QM S 78517) that is restricted to the Black Mountain boulder-fields. Although only three species are currently described, this genus is believed to be highly diverse, with all other species restricted to rainforest communities of northeastern Queensland (Robert Raven pers. comm.).

Discussion

The above examples outline narrowly distributed members of rainforest faunal groups that are now restricted to rock habitats in areas where rainforest is, or once was, largely absent or marginal. Extensive, layered rock habitat in mesic areas of Australia has a cool, moist rainforest-like microhabitat that is relatively buffered from short and long-term variation in temperature and moisture, and the effects of fire. The stability of these rock habitats means that they have acted as refugia for the persistence of rainforest lineages that may otherwise have disappeared from a region due to rainforest contraction resulting from climatic change. Rock habitats have therefore played an important role in maintaining the diversity of Australia's rainforest fauna.

The extent of rock outcrops plays a significant role in shaping animal distributions. Where rock occurs narrowly (i.e. as boulders along rainforest creek-lines or as isolated boulder fields), rock-restricted species have very small distributions (e.g. *Phyllurus* spp., *Orraya occultus*, *Cophixalus saxatilis* and *C. zweifeli*). However, where rock is extensive, as is the case with the granite outcropping of southeastern Queensland and northern NSW, the gorge systems flanking the Great Escarpment in coastal NSW, the Sydney Sandstones, or the Arnhem Land and Kimberley sandstone escarpments, rock-dwelling species tend to have much broader distributions (e.g. *Saltuarius wyberba* Couper, Schneider and Covacevich 1997, *S. moritzi* Couper, Sadlier, Shea and Worthington Wilmer 2008, *Phyllurus platurus* (Shaw 1790) and *Petropseudes dahl*).

Some groups of animals may be more capable of adapting to rock habitats. In many ways the rock habitats discussed herein are cave-like. Deeply layered rock, for

example the boulder mountains of north Queensland and the boulder-strewn creek-lines of mid-eastern Queensland, has numerous subterranean cavities. It has been suggested that geckos are “perhaps preadapted for the occupation of caves, owing to their chiefly nocturnal habits” (Bauer *et al.* 2002). The nocturnal habits of frogs and most of the other groups discussed herein are likely to confer similar advantages. One potential advantage of deep rock habitats is that they may extend the foraging periods of nocturnal species. Apart from nocturnal habits, there are numerous other factors that will determine the degree to which different faunal groups are able to adapt to rock habitats. Therefore, rock habitats are likely to have facilitated the persistence of a non-random subset of regional rainforest diversity. Finally, just as rock has enabled the persistence of rainforest lineages, it has no doubt provided a novel habitat to which open forest lineages have also adapted.

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